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The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*

Although cranial gracility is generally considered to be a characteristic feature of modern skulls, a quantification of the degree of development of cranial superstructures discloses varying levels of robusticity in certain recent and sub-recent populations. In order to account for these structures, biomechanical interpretations in terms of masticatory stress and the effects of structural constraints have been put forward. This paper examines the multivariate relationships between robusticity and cranial dimensions in modern humans through canonical correlation and principal components analyses. These analyses reveal a very significant association between robusticity and cranial size, by which the larger the size of the skull, the greater the development of the cranial superstructures. In this context, size is biased towards maximum cranial length, various measures of upper facial breadth, basion–nasion length and palato–dental size. A statistically less important relationship between robusticity and cranial shape reveals that there are two main circumstances in which a modern skull will develop superstructures, in either very large crania, independent of the breadth of the vault, or in very narrow ones with large teeth. The cranial superstructures are not only strongly influenced by certain cranial dimensions, but are inter-correlated in their expression. These morphological features should not be treated as independent phylogenetic traits.

The majority of recent crania are relatively small and gracile, clearly the result of a common temporal trend in the evolution of modern human cranial diversity. Although not unique in their level of robusticity among recent human groups, Australian aboriginals are the only population to show a relationship between robusticity and cranial breadth. It is suggested that the total morphological pattern observed in Australia does not reflect a plesiomorphic condition, but the specific history of occupation of that continent favouring size reduction with the maintenance of robusticity.

Finally, it is shown that most early modern fossils are comparatively large and robust. It is suggested that the definition of a modern cranial form should be disassociated from the concept of gracility, only observed in some recent human populations. © 1996 Academic Press Limited

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Introduction

The term ‘‘robust’’ is used to describe something ‘‘strongly formed or constructed’’. This concept also applies to the human skeleton, which can be more or less robustly built. In the post-cranial skeleton, robusticity is normally identified in the overall size of the individual, the cortical thickness of long bones and the development of the areas of muscle attachment. Interpretations of the presence and development of post-cranial robusticity are generally associated with mechanical factors related to physical activity (Frost, 1967, 1972, 1982; Little, 1973; Vaughn, 1981; Peck *et al.*, 1984). In the cranium, robusticity is not only described by overall size and bone thickness, but it is also expressed by a number of distinct features, like ridges, tori and tubercles. These features have been called the ‘‘cranial superstructures’’ (Weidenreich, 1940), and their presence, absence and degree of expression in different populations of modern and fossil hominids has been the subject of many studies. Although

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most of these studies offer only phylogenetic interpretations of these traits, there is a growing literature on studies of functional morphology, which includes works on the possible biomechanical origins of cranial superstructures. These works are always faced with the problems of identifying the ontogenetic and phylogenetic components within functional relationships, but they establish morphological units that co-vary in their growth parameters, and thus form units of phylogenetic change and inheritance.

This paper intends to contribute to both interpretative aspects of cranial morphology—functional and phylogenetic—by further integrating cranial robusticity with metrical dimensions. In order to do this, five aspects of the relationship between levels of robusticity and cranial size and shape will be examined—first, the character of such a relationship in terms of strength and constancy; second, the functional aspect of the variation observed; third, the regional distribution of cranial robusticity; fourth, the possible phylogenetic interpretations of both the relationship and the variation found; and last, implications for the current debate about modern human origins.

Cranial robusticity in man

Modern human crania vary markedly in size and shape. A large part of this variation can be attributed to populational differences, as groups differentiated in the course of their genetic response to environmental and demographic patterns through time. Accordingly, it is possible to use mathematical methods to identify crania from most modern populations on the basis of cranial measurements with a very high degree of certainty (Howells, 1973, 1989; Brace *et al.*, 1990; Pietrusewsky, 1990, 1992; Wright, 1992). Human skulls vary also according to level of robusticity. As mentioned above, cranial robusticity is partly expressed in the presence and degree of development of a number of morphological features. Some of these features of robusticity are relatively common in modern crania, like well-formed supraorbital ridges, rounded zygomatic trigones, zygomaxillary tuberosities, occipital crests and occipital tori. Others are much more rarely observed, like rounding of the infero–lateral margin of the orbit, pronounced sagittal or frontal keeling, retromastoid processes, posterior supramastoid tubercles, mastoid tubercles and asterionic processes, and are sometimes found in specific regional groups. Still others, are typically observed in fossil hominid groups and rarely or never in modern human skulls, like angular and supraorbital tori.

Functional relationships

As is the case in the post-cranial skeleton, the degree of robusticity of the human skull is also believed to be related to functional aspects of skeletal anatomy (Hrdlicka, 1910; Washburn, 1947; Moss & Young, 1960; Biegert, 1963; Aguirre & de la Macorra, 1964; Brace, 1964; Aguirre, 1968; Endo, 1970; Riesenfelt, 1974; Oyen & Enlow, 1981; Russell, 1985; Shea, 1986; Demes & Creel, 1988; Hylander *et al.*, 1991). However, the precise nature of the functional complex that underlies cranial robusticity is still a matter of debate.

Most studies have concentrated on the mechanical role of the supraorbital ridges/torus of hominids. Contrary to the occipital torus and occipital crest, the anatomical form of the supraorbital ridges/torus is not directly defined by the insertion and/or function of specific muscles or ligaments. Therefore, most functional interpretations consider this structure part of the stress resistance architecture of the skull. Endo (1965, 1966, 1970) demonstrated experimentally that the supraorbital area is mechanically deformed (bent) during biting. He postulated a model by which the facial skeleton acts as a rigid frame (beams) through which the upward forces generated during biting are transferred to the supraorbital region, which also receives the downward bilateral pull of the temporal muscles. Endo further postulated that anterior dental loading was the main ‘‘stressing’’ force. Endo’s studies were developed by Russell (1983, 1985), who found that it is the intermittent masticatory stress throughout an individual’s life which stimulates cortical bone remodelling directed to acquiring a shape that counteracts the stress by minimizing the bending effect. Russell (1985) concluded that ontogenetic development of the supraorbital area will result in the bending stresses being neutralized by opposite structural curves. Russell did not include dental dimensions in her model, but Demes & Creel (1988) showed that bite force depends on both the magnitude of the muscle force (which in turn depends on the specific dimensions that determine the load and lever arms of the contractile movement) and the occlusal pressure (dental area). Therefore, it is expected that dental dimensions will also be related to facial robusticity. Furthermore, Oyen *et al.* (1979*a*) found that rapid development of the supraorbital ridges coincides with dental eruption, and Oyen *et al.* (1979*b*) postulated that dental eruption changes the lever-arm:load-arm ratio, which changes the relation between masticatory muscles and the facial skeleton. Hilloowala & Trent (1988*a*,*b*) developed this further by arguing that it is the force needed to elevate the mandible acting as a lever that determines the relationship between the supraorbital region of the skull and the masticatory apparatus through the pulling action of the anterior fibres of the temporalis. However, contrary to Endo and Russell, Hilloowala & Trent (1988*b*) argue that it is not only anterior dental loading that creates the upward stressing forces, but that the posterior dentition is also involved.

There have been criticisms of Endo’s localized stress hypothesis (Picq & Hylander, 1989). A number of researchers have suggested that supraorbital tori develop not to counteract masticatory stress, but to fill the area between the brain and the face; in other words, supraorbital tori have a spatial role (Moss & Young, 1960; Biegert, 1963; Shea, 1986). This spatial model has received strong support from the morphometric studies of Ravosa (1988, 1989, 1991) and the *in vivo* strain analysis in primates carried out by Hylander and co-workers (Hylander, 1984; Hylander *et al.*, 1991). Hylander *et al.* (1991) find that the glabellar region of the frontal bone is indeed strained by mastication (equally by biting and chewing), but that this strain is very low, lower than in other portions of the facial skeleton. Although acknowledging that bone requires certain repeated levels of strain to complete its development, these authors do not accept that larger supraorbital tori are the result of structural adaptations to counteract greater masticatory stress. They argue that supraorbital ridges only perform a spatial function, a point that also explains the low levels of strain along the area.

These different studies indicate that there is a functional relationship underlying supraorbital development, whether directly associated to masticatory stress or to spatial arrangements, or both. However, many important points remain unresolved. The first is whether the features of robusticity like supraorbital and occipital tori, act as cranial superstructures with a common underlying relationship; second, whether the parameters underlying such a relationship are equally applicable in all modern populations; and third, whether it is ontogenetic or phylogenetic components of variation that determine most of the relationships observed.

Temporal and spatial patterns

Throughout the course of human evolution, features of robusticity like supraorbital and occipital tori, have been acquired, lost or changed in different groups, so that the recording of their presence, absence and character has been a useful tool in phylogenetic reconstructions.

As an example, it is possible to characterize populations of *Homo erectus* by the presence of a pronounced, horizontal supraorbital torus and supratoral sulcus on the frontal bone, while a morphological description of the Neanderthal population of the late Middle and Upper Pleistocene of Europe will certainly include the presence of a supraorbital torus that follows the contour of the orbits, arching over the middle portion of the supraorbital area. Modern humans, however, are not clearly characterized by their supraorbital morphology or by any other feature of robusticity as other hominid populations. Although most descriptions of modern *Homo sapiens* will include skeletal gracility as a characterizing trait, differing levels of robusticity are observed among recent and fossil modern skeletons. Early modern fossils have crania that are robust in relation to most recent populations—specimens like Omo I, Qafzeh 9 and 6, Skhul 4 and 5, and the fragmentary remains from Klasies River Mouth, show features like strong supraorbital ridges, which may form a real continuous torus, strong zygomaxillary tuberosities, developed zygomatic trigones and pronounced occipital tori. These traits have been mainly lost among recent populations, except in a few groups like Australian, Fueguian and Patagonian aborigines that continue to express high levels of cranial robusticity to the present. In these groups, cranial robusticity is interpreted as a plesiomorphic trait. Therefore, there has been a process of skeletal gracilization in modern humans that can be identified in most recent groups, although not a universal feature of the species, either temporally or geographically. These aspects of the evolution of a modern skull are intimately linked to the evolution of cranial diversity through the differential retention of robusticity in recent populations.

Robusticity and cranial metrical dimensions

As mentioned before, several studies have examined the relationship between supraorbital torus development and certain cranial dimensions (Russell, 1983, 1985; Demes & Creel, 1988; Hilloowala & Trent, 1988*a,b*). In anatomical terms, the results of these investigations may be summarized as follows: there is an apparent relationship between dental size (anterior and posterior dentition), mandibular length, temporal fossae area and minimum frontal breadth with supraorbital torus/ridge development. Furthermore, facial angle may also be correlated under conditions of great stress production (Russell, 1985). Lahr (1992, 1996) examined the relationship between the degree of expression of several features of robusticity, scored non-metrically, with metrical craniodental dimensions, and found that it is possible to predict the degree of expression of cranial robusticity in terms of cranial measurements with close to 100% accuracy. For many of the features under study, some of the cranial measurements responsible for most of the discrimination between the degrees of development of superstructures were the dimensions of the posterior dentition and of the cranial attachment of the *temporalis*, suggesting a close relationship between masticatory power and cranial robusticity. In spite of these results that would support the localized masticatory stress hypothesis, the presence of many other cranial variables in the discriminant functions highlights the role of cranial dimensions in the expression of cranial superstructures. Furthermore, like previous studies, Lahr (1992) analysed each of the features of robusticity independently, and although the metrical variables responsible for discriminating each trait were not exactly the same in each case, there were enough discriminating variables in common to suggest that at least the facial superstructures (supraorbital ridges, zygomatic trigone, depth of infraglabellar notch and zygomaxillary tuberosity) may respond to a single functional complex.

The following analyses attempt to address these issues by carrying out a more integrated study of the relationship between cranial measurements and robusticity. First, the existence of a close relationship between overall cranial robusticity (scored non-metrically for nine separate features) and craniodental metrical dimensions will be investigated, thus determining the relative importance of the metrical and non-metrical traits studied in the morphological variability observed. Second, the main underlying variables defining the relationship between robusticity and cranial dimensions will be examined for possible anatomical interpretations. Last, the geographical distribution of recent patterns of cranial robusticity will be described.

Materials and methods

This study was carried out using a complete data set of cranial and dental measurements derived from several modern populations and a few individual fossils. Mandibles were not used because they are too frequently missing, and the samples are unsexed. Only for the discussion of the relationship between robusticity and sexual dimorphism, the levels of robusticity in males and females of two populations (Inuit and Fueguian) are compared. The number and composition of these two cranial series, representing restricted populations, enabled confident sexing of the skulls. The exact number and composition of the samples used varied according to whether dental measurements were included or not, varying from 198 to 134 individuals in the first and second canonical correlation analyses, respectively. The principal component analysis (PCA) used the same sample as the second canonical correlation analysis. Variables with high frequencies of missing values were omitted, in order to maximize the number of crania in the samples. The geographical origin of these samples is described in Table 1.

Two different sets of variables were obtained from each skull. The first one was composed of cranial measurements as described in Howells (1973), palatal length, a measure of the distance from the position of minimum frontal breadth to the face and the distance between left and right temporal muscles across the vault as described in Lahr (1992), and buccolingual dimensions of the first and second upper molars. In order to maximize sample size, the dental dimensions were taken as the mean of left and right measurements, or either the left or right value when the tooth was present in one side only. This procedure is justified on the basis of the high correlation between left and right buccolingual values for the first and second molars (M1: $r=0{\cdot}9694$, $P<0{\cdot}001$, $n=182$; M2: $r=0{\cdot}9528$, $P<0{\cdot}001$) in the sample used (where teeth from both sides are present). The second set of variables refers to the measurement of cranial robusticity, and it used ordinal grades to score degree of development. The features of robusticity examined were the development of the supraorbital ridges, zygomatic trigone, zygomaxillary tuberosity and sagittal keeling, the depth of the infraglabellar notch, degree of rounding of the infero–lateral margin of the orbit, and categories of nasal saddle, occipital torus development and occipital crest (Figure 1). The grades and scoring procedure of each of these traits may be found in Lahr (1992, 1994, 1996). The complete set of metrical and non-metrical variables used is listed in Table 2.

Statistical analyses

The study of the relationship between a set of metric variables, representing cranial dimensions, and a set of non-metric variables, representing robusticity, was carried out through canonical correlation analyses. Canonical correlation methods will reveal the correlation underlying metric and non-metric variables as two sets, and answer the question of

Table 1 **Composition and size of the samples used in the canonical correlation (CC) and principal components (PC) analyses**

Region	1st CCA	2nd CCA/PCA
Europe	19	13
North Africa	7	3
Africa south of the Sahara:		
East Africa	6	7
West Africa	9	7
South Africa (bushman)	6	5
India	2	1
Southeast Asia		
Southeast Asia	20	14
Andaman Islands	4	3
East and Northeast Asia	25	12
Inuit	5	4
American Indian:		
North American Indian	1	1
South American Indian	3	—
Fueguian/Patagonian	25	12
Polynesian	6	3
Island Melanesia	5	2
Australia	32	27
Mediterranean Epi-Palaeolithic:		
Afalou	13	9
Taforalt	3	4
Natufian	3	3
Pleistocene fossils:		
Zhoukoudian UC (China)*	2	1 (UC 103)
Liujiang*†	1	1
Ohalo (Israel)	1	1
Nahal Ein Gev (Israel)	1	1

*Measured from casts at The Natural History Museum, London.
†The Liujiang fossil has no precise date (Brown, 1992).

how the sets can be combined to make the correlation between components of the two sets a maximum. If the first canonical correlation is statistically significant, there is at least one way in which the domains of metric and non-metric variables are related (Cooley & Lohnes, 1962). Most users will want to examine the relationship between the original variables and the canonical vectors, but as Wherry (1984: pp. 300–301) points out, some workers have caused confusion by trying to interpret the sets of variable weights to interpret the results. The correct procedure is the use of the structure coefficients, which are the loadings of the variables on the canonical vectors of the sets.

Redundancy coefficients of Stewart and Love are an alternative measure of association between two sets of variables. Unlike the canonical correlation coefficients, these measures are asymmetrical with respect to the two sets. Redundancy coefficients measure the proportion of variance of the variables in the relevant set that is accounted for by the corresponding canonical variate. As Tatsuoka (1988) points out, redundancy coefficients can play an important role in modifying enthusiasm about the canonical correlation coefficient. We can think of redundancy coefficients as measuring the overlap between the two sets of variables (Timm, 1975). The redundancy measure can also be interpreted as a measure of the extent to which one set of variables (either metric or non-metric) can be reconstructed from knowledge

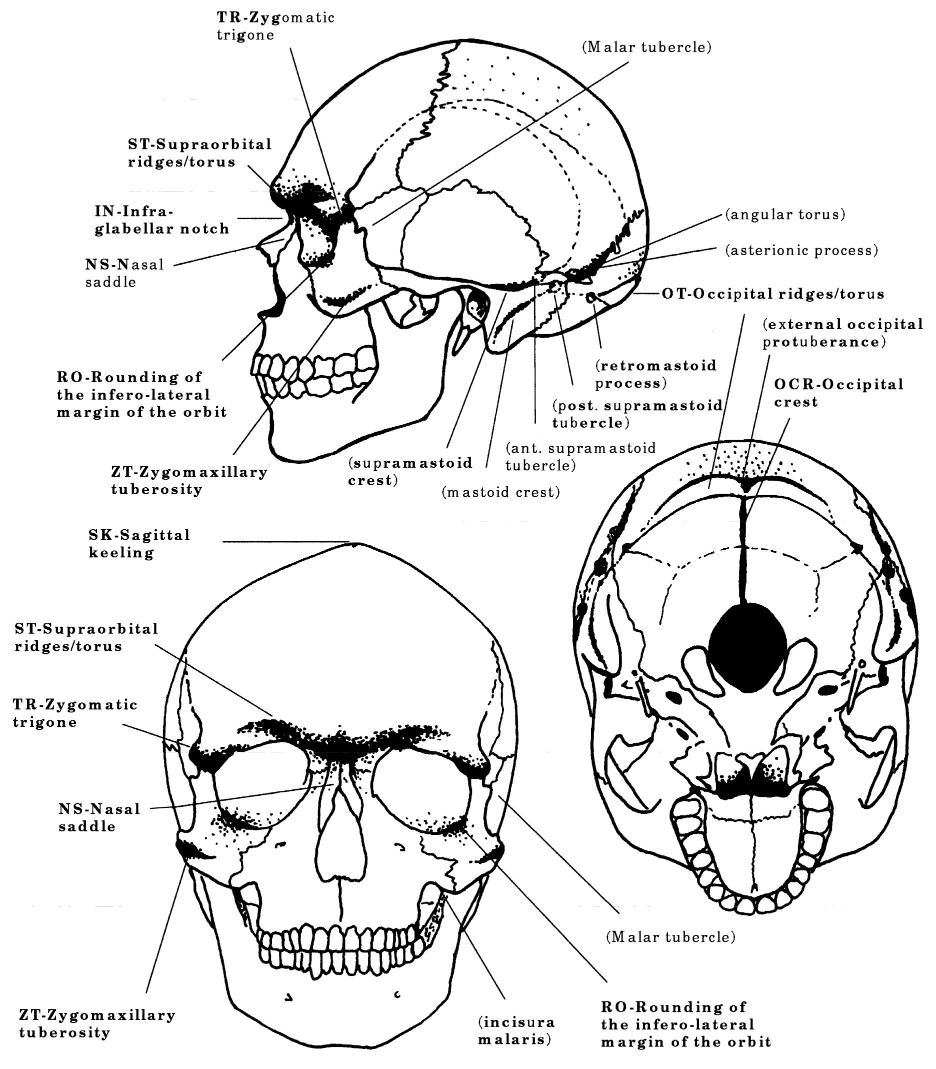

TR-Zygomatic trigone
(Malar tubercle)
ST-Supraorbital ridges/torus
IN-Infra-glabellar notch
NS-Nasal saddle
(angular torus)
(asterionic process)
OT-Occipital ridges/torus
(external occipital protuberance)
RO-Rounding of the infero-lateral margin of the orbit
(retromastoid process)
OCR-Occipital crest
(post. supramastoid tubercle)
(ant. supramastoid tubercle)
ZT-Zygomaxillary tuberosity
(supramastoid crest)
(mastoid crest)
SK-Sagittal keeling
ST-Supraorbital ridges/torus
TR-Zygomatic trigone
NS-Nasal saddle
(Malar tubercle)
ZT-Zygomaxillary tuberosity
(incisura malaris)
RO-Rounding of the infero-lateral margin of the orbit

Figure 1. Cranial superstructures. In bold, the features of robusticity scored as ordinal grades and used in the present study. In parentheses, other tubercles and tori of the human skull not included in the present analysis.

about the other set (Green, 1978). A textbook by Green (1978) provides a clear and integrated description of canonical correlation analysis, with an example worked from the raw data (not just from the correlation matrix).

The much better known technique of PCA (Green, 1978) was performed on the same data set and using the same variables as the second canonical correlation analysis. PCA ignores the differences in variable types (whether metric or nonmetric) and seeks only to maximize explained variance, regardless of the *a priori* sets of variables. Given the different aims of

Table 2 Metrical and non-metrical variables used in the study

Metrical

- (a) Description in Howells (1973)
  - GOL—maximum cranial length
  - BNL—basion–nasion length
  - XFB—max. frontal breadth
  - ASB—asterionic breadth
  - NPH—nasion–porion height
  - NLB—nasal breadth
  - OBB—orbital breadth
  - MAB—maxillary breadth
  - BPL—basion–porion length
  - SSS—subspinale subtense
  - NAS—nasion subtense
  - FRC—frontal chord
  - PAC—parietal chord
  - OCC—occipital chord
  - GLS—glabellar subtense
  - FRF—frontal subtense-fraction
  - PAF—parietal subtense-fraction
  - NOL—naso–occipital length
  - BBH—basi–bregmatic height
  - XPB—max, parietal breadth
  - AUB—biauricular breadth
  - NLH—nasal height
  - OBH—orbital height
  - JUB—bijugal breadth
  - WMH—min. malar height
  - ZMB—bimaxillary breadth
  - FMB—bifrontal breadth
  - EKB—biorbital breadth
  - FRS—frontal subtense
  - PAS—parietal subtense
  - OCS—occipital subtense
  - SOS—supraorbital subtense
  - OCF—occipital subtense-fraction
- (b) Description in Lahr (1992)
  - WIOB: minimum interorbital breadth
  - PALL: palatal length
  - WFBZFS: distance position of minimum frontal breadth and the zygomatico–frontal suture
  - SILLPA: distance between left and right temporal muscles across the vault
  - BLM1: buccolingual upper first molar length
  - BLM2: buccolingual upper second molar length
- *Non-metrical (features of robusticity)
  - ST: development of the supraorbital ridges and formation of a supraorbital torus
  - TR: development of the zygomatic trigone
  - IN: depth of the infraglabellar notch
  - NS: categories of nasal saddle
  - ZT: development of a zygomaxillary tuberosity
  - RO: rounding of the infero–lateral margin of the orbit
  - SK: degree of sagittal keeling
  - OT: configuration of the superior and supreme nuchal lines and formation of an occipital torus
  - OCR: development of an occipital crest

*Description of grades and scoring techniques in Lahr (1992, 1994, 1996).

canonical correlation and PCA, a comparison of the results obtained through these two techniques provides a good test of the findings.

The program for canonical correlation analysis is written by one of us (R.S.V.W.), as an auxiliary program for the MV-NUTSHELL package for archaeological analysis. The program for PCA comes from the distributed version of MV-NUTSHELL (Baxter, 1994; Wright, 1994).

Results

The relationship between cranial robusticity and cranial dimensions

The results of the first canonical correlation analysis on 198 crania using all the non-metrical features of robusticity and a set of cranial metrics show that the non-metrical and metrical variable sets are correlated: canonical correlation of factor 1:0·85. This correlation is highly significant ($\chi^2 = 525{\cdot}74$; $P < 0{\cdot}0001$). The variable loadings show that the first canonical vector

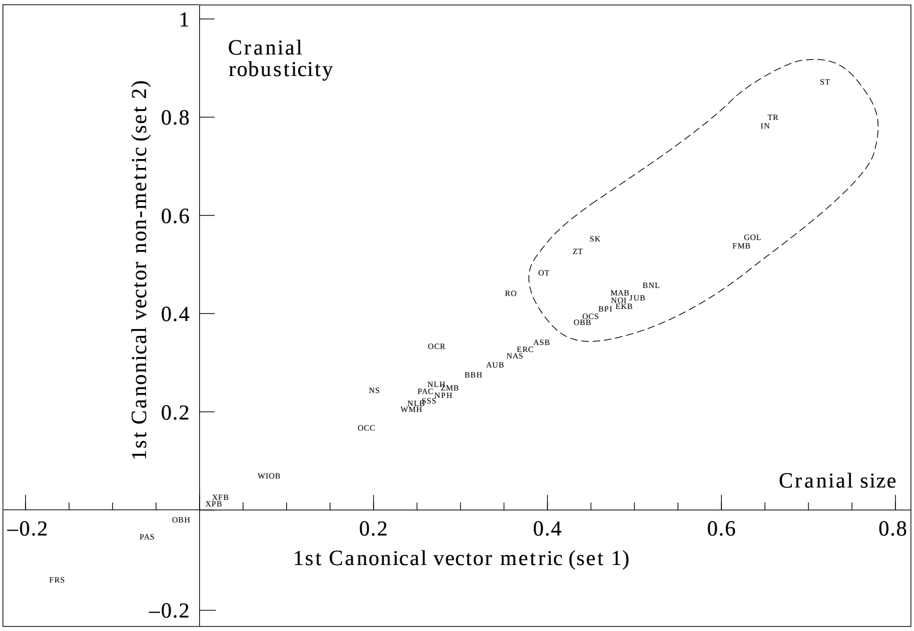


Figure 2. Plot of variables along the metric and non-metric vectors of the first canonical variate correlating cranial measurements and overall robusticity (measured as grades of expression of nine morphological features). Area in dotted line, metrical and non-metrical variables moderately to highly correlated with the first canonical variate.

relates overall cranial size with intensity of non-metrical traits (robusticity), i.e. the bigger the crania the more robust and vice-versa (Figure 2). The metrical traits that are moderately to strongly correlated with the first canonical vector (correlations larger than 0·4) are maximum length (GOL, NOL), upper facial breadth (FMB, JUB, EKB, OBB), facial–basal length (BNL), palatal size and protrusion (MAB, BPL), and occipital flexion (OCS). The variable loadings for the features of robusticity vary from 0·203 in the case of categories of nasal saddle to 0·732 in the case of development of the supraorbital ridges, i.e. there is a lot of variation in the level of correlation of the various non-metrical features used. The loadings on the first canonical variate are monopolar, i.e. they are either positive or close to zero (those close to zero are not correlated with the first vector). These results show that the main correlation of cranial robusticity is not with a metrical shape factor, but with cranial size (chiefly represented by length and upper facial breadth). The redundancy values show that 24·9% of the non-metrical variance is explained by the metrical vector, whereas only 9·8% of the variance in metrical dimensions is accounted for by the non-metric vector. These values indicate that the direction of influence is from the metrics to the non-metrics, i.e. robusticity increases as cranial size increases (length and upper facial breadth), but the reverse effect is much weaker.

The discussion now turns to interpreting the crania plotted on the scattergram. For the purpose of exposition, somewhat arbitrary lines are drawn to define ‘‘groups’’. These groups are examplars, not groups derived by any formal technique such as cluster analysis.

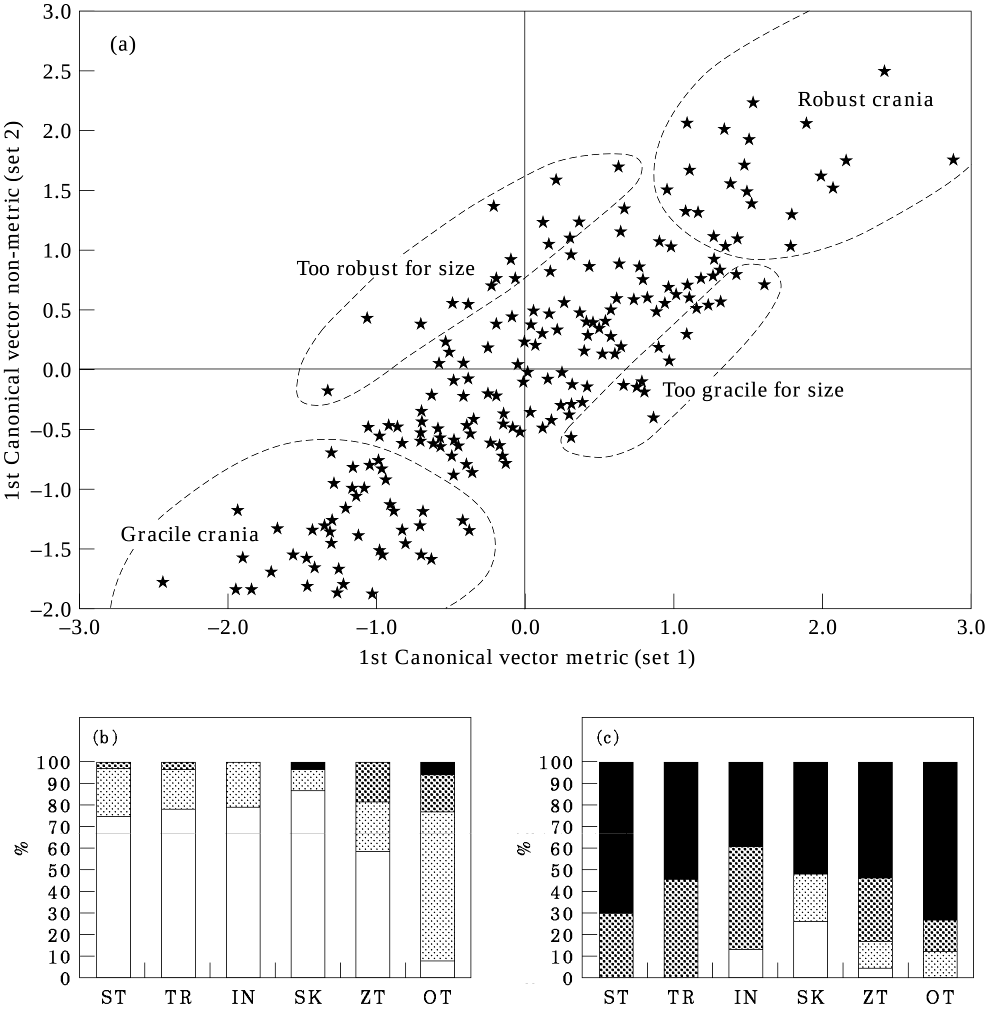
Two anatomical groups defined by the relationship between cranial size and robusticity can be identified, one group composed of large and robust crania, and another one of small and gracile skulls, circled in the upper right and lower left quadrants of Figure 3 respectively. It is also possible to identify two groups of crania that depart in opposite ways from the relationship, i.e. crania that are either too robust or too gracile for their size. As shown by the mean value of cranial and frontal breadth in both the robust and gracile groups (Graciles: XPB: $\bar{x} = 137$ mm, XFB: $\bar{x} = 115$ mm; Robusts: XPB: $\bar{x} = 136$ mm, XFB: $\bar{x} = 114$ mm), cranial breadth does not play any role in the definition of the observed relationship between robusticity and size.

The relationship between facial robusticity and craniodental dimensions

In order to examine whether there is a closer functional relationship underlying the development of only the facial superstructures (excluding features like occipital torus and occipital crest from the non-metric set of data), a second canonical correlation was performed. This included only features of facial (development of supraorbital ridges, zygomatic trigone, zygomaxillary tuberosity, rounding of the infero–lateral margin of the orbit and depth of infraglabellar notch) and vault (sagittal keeling) robusticity. Because of the potentially important role of masticatory stress in the degree of development of these features, two measures of dental size (buccolingual M1 and M2), palatal length, a measure of proximity of left and right temporal muscles across the vault and a measure of the position of minimum frontal breadth relative to the face were included in the metrical set of variables. The inclusion of dental measurements in the analysis unavoidably reduced the sample size. This analysis was performed on a data set of 134 skulls.

The canonical correlation between cranial metrical dimensions and facial robusticity was very strong (canonical correlation of factor 1:0·90). All the features of robusticity examined (ST, TR, IN, ZT and SK) show moderate to strong positive loadings on the first canonical variate, suggesting that they follow a common underlying relationship with the metrical variables. The metrical variables with moderate to high loadings on the first vector are similar to the ones found in the first analysis [Figure 4(a)]—maximum length (GOL, NOL), maxillary breadth (MAB), upper facial breadth (OBB, FMB, EKB, JUB), facial–basal length (BNL), but also include specific features of the supraorbital region, like glabellar protrusion (GLS) and the distance between position of minimum frontal breadth and the zygomatico–frontal suture (WFBZFS), and palatodental dimensions (PALL, BLM1, BLM2). The redundancy results indicate that the relationship obtained between the metrical dimensions and the facial features of robusticity is stronger, 37·2% of the variance in robusticity is explained by the metric set of variables, and 11% of metrical variation is explained by variation in facial robusticity.

The second canonical correlation has a value of 0·77, and it is also significant ($\chi^2 = 340{\cdot}72$; $P < 0{\cdot}0001$). This second canonical variate is orthogonal to the first, and naturally describes crania that have a very different relationship between facial robusticity and metrical dimensions. The variables with moderate positive loadings (0·3–0·6) on the first factor of the second canonical variate are only two: sagittal keeling (SK) and orbital height (OBH), and with negative loadings ($-0{\cdot}3$–$-0{\cdot}6$) are minimum interorbital breadth (WIOB), distance between left and right temporal muscles across the vault (SILLPA) and rounding of the infero–lateral margin of the orbit (RO). The variables correlated significantly on the second factor of the second canonical variate are the same as on the first, with the difference that the loading of sagittal keeling is higher. The correlation of variables along the second canonical variate is bipolar, i.e. there are both positive and negative high loadings, and indicates that this variate identified a ‘‘shape’’ factor associating keeling of the vault and certain dimensions [Figure 4(b)]. The metric factor accounts for 7·3% of the variance in the non-metric variables, while



Gracile group			
GOL:	175.0	OBB:	40.0
NOL:	174.0	MAB:	62.0
BNL:	96.0	BPL:	94.0
JUB:	120.0	OCS:	26.0
FMB:	96.0		
EKB:	95.0	XPB:	137.0
		XFB:	115.0

Robust group			
GOL:	190.0	OBB:	43.0
NOL:	184.0	MAB:	68.0
BNL:	103.0	BPL:	103.0
JUB:	120.0	OCS:	30.0
FMB:	105.0		
EKB:	101.0	XPB:	136.0
		XFB:	114.0

Figure 3. (a) Plot of crania along the first canonical variate, separating robust crania on the upper right-hand quadrant from gracile ones on the lower-left quadrant. Histograms and box metrical values refer to the crania circled on the two extremes of the plot (the robust and gracile groups). The histograms [(b) gracile crania; (c) robust crania] show the expression of robusticity of the six non-metric grade features in these two groups of crania, ranging from very pronounced (black) to absent (white). The boxes show the mean values of the traits moderately to strongly correlated with the metric vector, whereas the mean values of XPB and XFB illustrate the absence of correlation of these variables with the first canonical vector obtained.

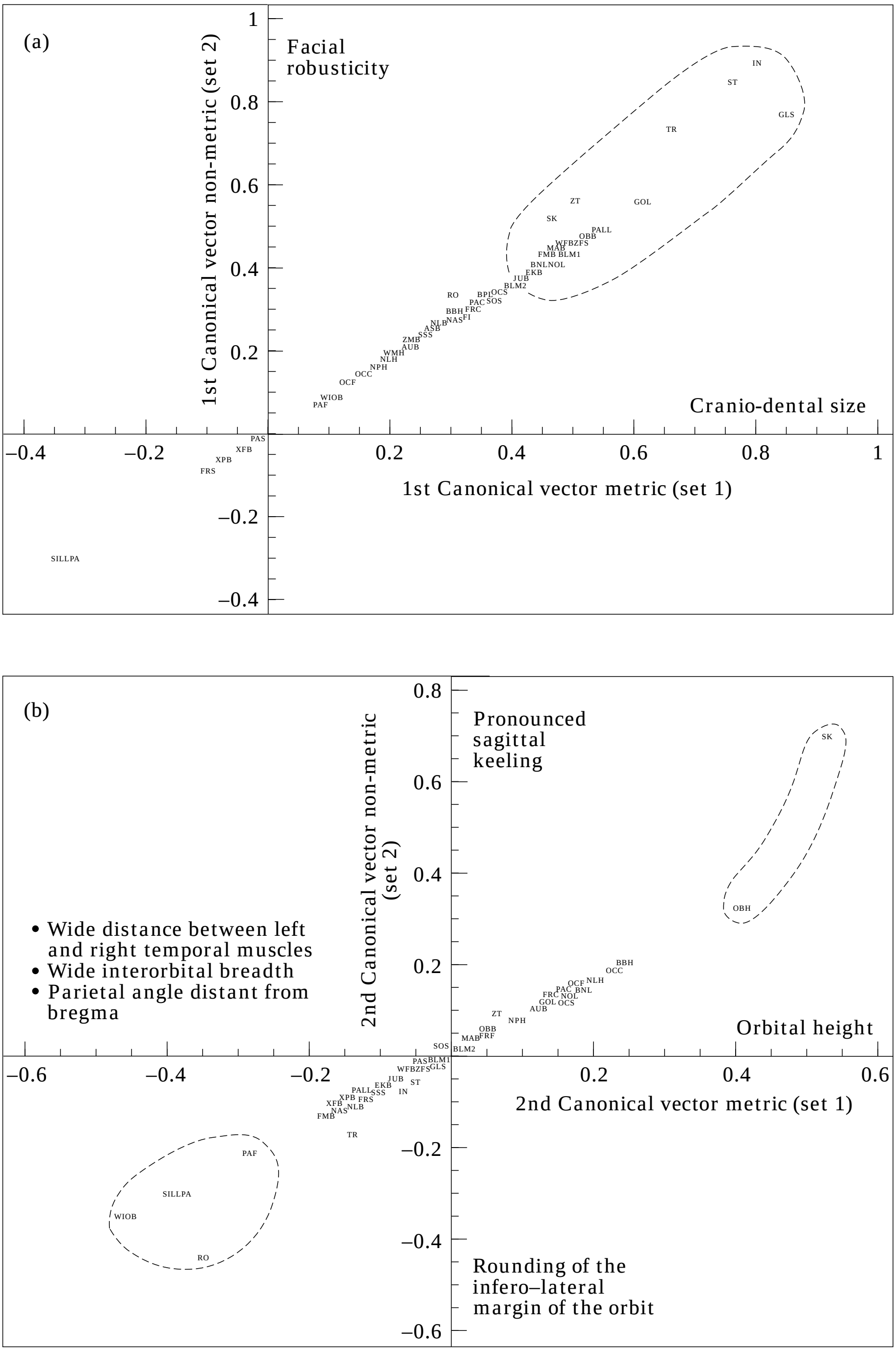


Figure 4. (a) Plot of variables along the metric and non-metric vectors of the first canonical variate correlating cranial–dental measurements and craniofacial robusticity (measured as grades of expression of six morphological features). Area in dotted line, metrical and non-metrical variables moderately to highly correlated with the first canonical variate; (b) plot of variables along the metric and non-metric vectors of the second canonical variate correlating cranial–dental measurements and craniofacial robusticity (measured as grades of expression of six morphological features).

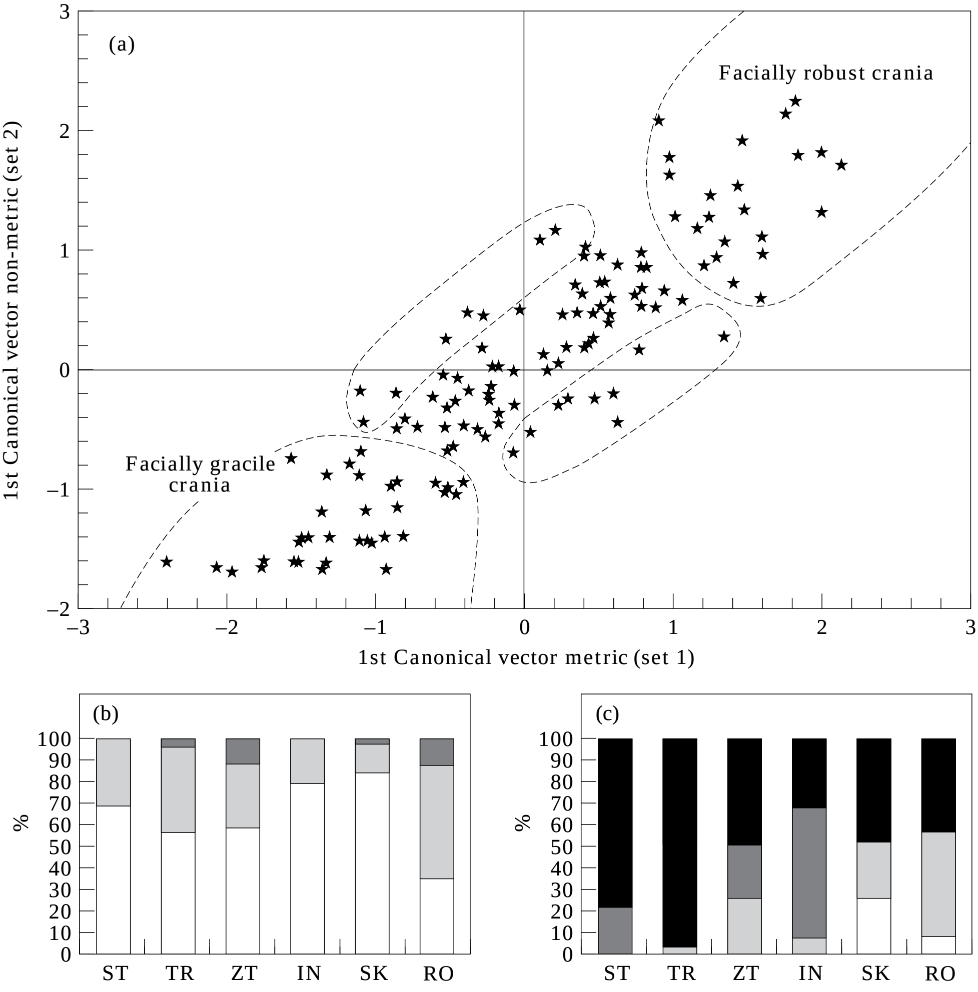
the non-metric factor accounts for 1·8% of the variance in the metric variables. Therefore, this second canonical variate identified a very specific relationship that discloses a cranial shape associated with the development of keeling of the vault: pronounced sagittal keeling is correlated significantly with high orbits, narrow inter-orbital widths, spatially close temporal muscles across the vault and rounding of the infero–lateral margin of the orbit. Taken together, the relationships identified in the first and second canonical variates account for 44·5% of the variation in craniofacial robusticity.

As with the first canonical correlation analysis, the results of this second analysis using only facial superstructures in the non-metric vector allow the identification of facially robust and gracile skulls (Figure 5). The individual composition of these two groups is very similar to the robust and gracile groups of Figure 3, although not identical. Both groups (robust and gracile) of Figure 5 contain individuals that were outside the circled areas in Figure 3, but on the other hand, except for a single skull, all the crania that were classified as either robust or gracile in Figure 3 and used in the second canonical correlation analysis, are within the facially robust or gracile groups of Figure 5. This would suggest that most skulls show a similarly distinct pattern of cranial and facial robusticity (either gracile or robust), but that in a few skulls facial robusticity or the absence of, is more pronounced than the overall cranial pattern. This further reinforces the view that the degree of expression of each feature is correlated with the individual's level of robusticity, although certain groups of features like the facial traits analysed in the second canonical correlation, form a recognizable morphological complex.

PCA analysis

A PCA was performed using the same data and variable set as the second canonical correlation. The results of this analysis are very similar to those obtained in the canonical correlation analyses. The metrical variables that have a strong positive loading on the first principal component (GOL, JUB, FMB, EKB, NOL, MAB, BNL, OBB, ZMB, AUB, BBH, FRC) are mostly the same that have strong or moderate loadings on the first canonical variates of the canonical correlations, although the features of facial robusticity and sagittal keeling are only moderately correlated with the first principal component. This component accounts for 27·3% of the total variance, and may be said to represent cranial size as defined before in terms of maximum cranial length, upper facial breadth, palatal size and facial–basal length, and a few other main cranial dimensions, like basal breadth, cranial height and frontal length. As was the case for the first canonical variate, the loadings on the first principal component are mainly positive or close to zero, confirming that the main structure in the data is one of metric size correlating with robusticity and the reverse.

The second principal component, which accounts for 11·4% of the variance, is different in character from the first in the sense that the variables have both positive and negative loadings on this factor (like the second canonical variate). In other words, there is a shape component involved. The variables with moderate to strong positive loadings on PC2 are all related to width dimensions (XPB, XFB, SILLPA, AUB), whereas those with moderate negative loadings are related to robusticity, palatodental size and protrusion, and position of minimum frontal breadth (TR, IN, RO, ST, BLM1, BLM2, SSS, PALL, WFBZFS). Therefore, the ''shape'' relationship disclosed by the second PC is different from that identified in the second canonical variate. It contrasts broad and gracile crania with robust and narrow ones, and it shows the close association between degree of facial robusticity and dental size. Orthogonal plots of the variables along principal components 1 and 2 show the features described above (Figure 6).



Gracile group

GLS:	1.8	EKB:	96.0
GOL:	175.0	JUB:	112.0
NOL:	174.0	PALL:	53.0
BNL:	96.0	MAB:	62.0
WFBZFS:	17.0	BLM1:	11.6
OBB:	40.0	BLM2:	11.7
FMB:	96.0		
		XPB:	137.0
		XFB:	115.0

Robust group

GLS:	5.9	EKB:	102.0
GOL:	190.0	JUB:	121.0
NOL:	185.0	PALL:	59.0
BNL:	104.0	MAB:	69.0
WFBZFS:	24.0	BLM1:	12.8
OBB:	44.0	BLM2:	13.1
FMB:	105.0		
		XPB:	136.0
		XFB:	114.0

Figure 5. (a) Plot of crania along the first canonical variate, separating facially robust crania on the upper right-hand quadrant from facially gracile ones on the lower-left quadrant. Histograms and box metrical values refer to the crania circled on the two extremes of the plot [(b) gracile and (c) robust groups]. The histograms show the expression of robusticity of the six non-metric grade features in these two groups of crania, ranging from very pronounced (black) to absent (white). The boxes show the mean values of the traits moderately to strongly correlated with the metric vector, whereas the mean values of XPB and XFB illustrate the absence of correlation of these variables with the first canonical vector obtained.

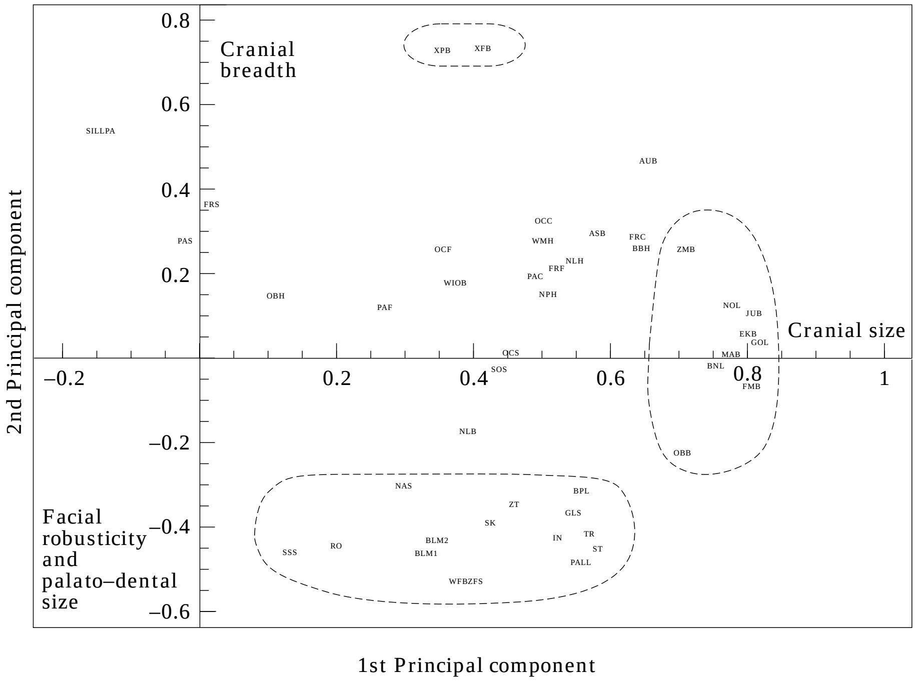


Figure 6. Plot of variables on the first and second principal components, showing the correlation of cranial size on PC1 and cranial shape on PC2.

The anatomical interpretation of this plot is complicated by the correlation of robusticity on both the first and second principal components, so that it is possible to find both broad and narrow skulls that are relatively robust (Figure 7).

In order to interpret the spatial distribution of skulls along the first and second principal components, a combination of the size (represented by cranial length, upper facial breadth and facial–basal length) and shape variables was used to delineate arbitrary groups of crania with corresponding metrical dimensions (Figure 7). Table 3 shows the mean values of the metrical variables used to define these groups (those strongly correlated with PC1 and PC2) for the 12 groups obtained. The most peripheral groups present comparatively extreme morphologies, whereas the four central groups (C, E, H, K) are less differentiated. The four internal groups comprise 64·9% of the crania studied. Figure 8 shows the gradient of robusticity visible from the upper left quadrant of Figure 7 (groups A and D) towards the lower right one (groups G and I). It is clear that the broad short skulls show the smallest development of facial robusticity, whereas both the very narrow, but not particularly large, skulls of group G and the long and narrow skulls of group I, show a very pronounced expression of facial robusticity.

Regionality in recent cranial robusticity. The regional distribution of overall cranial robusticity can be examined if the crania in Figures 3 and 5 are identified by population of origin. The group of skulls circled in the upper right quadrant of Figure 3, i.e. robust crania, are 23 in all: 15 Australians (65·2%), three Fueguians/Patagonians (13·0%), two Afalou/Taforalt (8·7%), one Ainu (4·3%), one Maori (4·3%) and Zkn UC 101 (4·3%). The regional composition of the group of skulls with pronounced facial robusticity (circled in the upper right quadrant of Figure

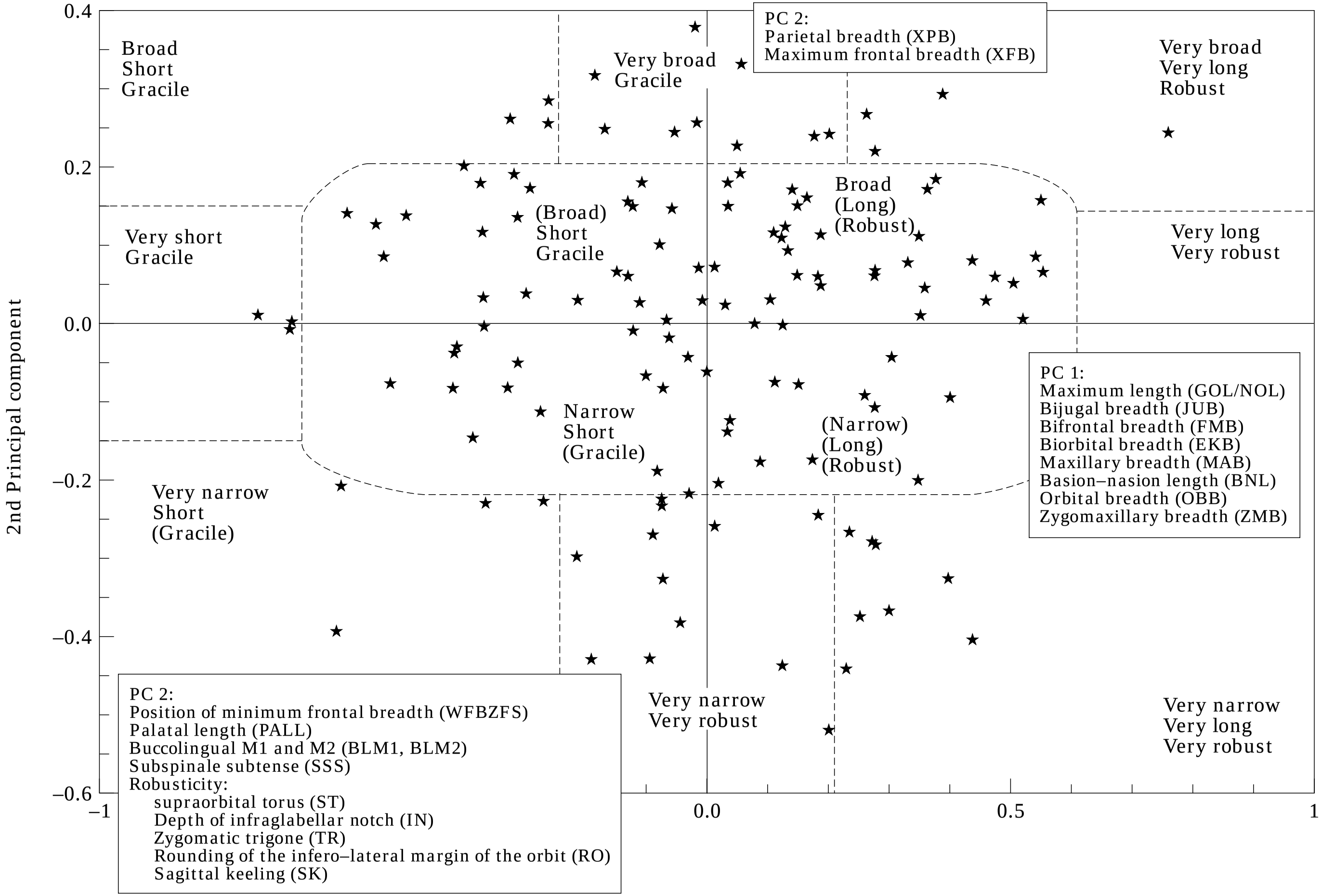


Figure 7. Plot of crania on the first and second principal components, showing small to large skulls distributed from left to right along PC1, the separation of broad and narrow skulls along PC2, and the 12 groups resulting from the spatial combination of variables along PC1 and PC2.

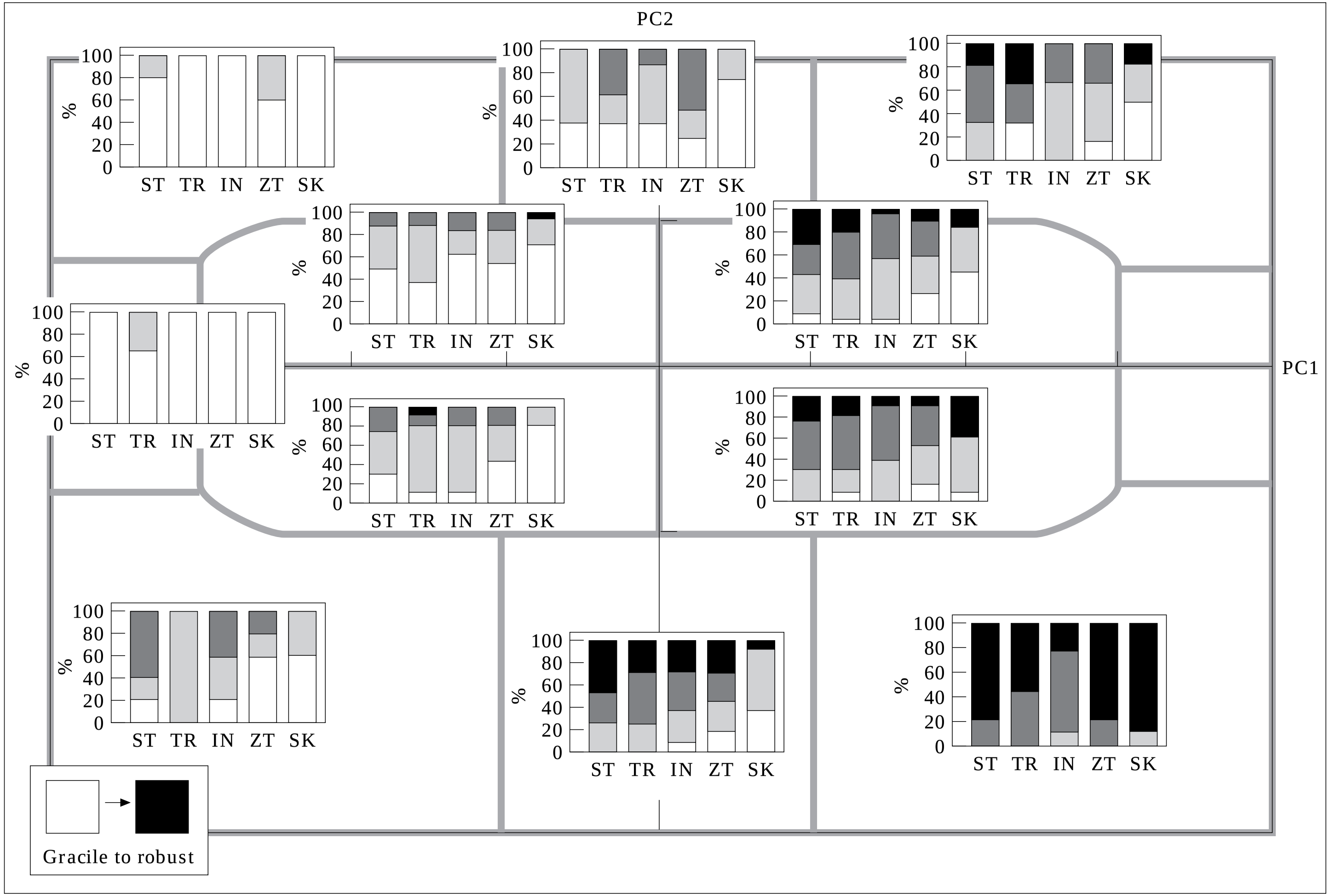


Figure 8. Histograms showing the expression of robusticity in craniofacial traits (ST, TR, IN, ZT, SK) in the 12 groups defined in Figure 8, forming a gradient from gracile crania on the upper left quadrant (broad and short skulls) to very robust ones on the lower right quadrant (long and narrow skulls).

Table 3 Average values of some of the metrical variables strongly correlated with the first and second principal components for the 12 groups defined by the plot of crania along PC1 and PC2

Group	GOL	JUB	MAB	BNL	AUB	BBH	FRC	XPB	XFB	BLM1	BLM2	WFBZFS	SILLPA
(A) Broad short gracile	173	110	63	97	118	132	112	141	120	11·4	11·5	**15**	**119**
(B) Broad gracile	182	114	67	98	126	134	113	144	123	11·7	11·7	**15**	109
(C) (Broad) short gracile	176	114	63	97	121	131	109	138	115	11·8	12·0	17	101
(D) V. short gracile	**167**	**102**	**57**	**90**	110	**121**	105	135	109	**11·1**	**11·1**	17	99
(E) Narrow short (gracile)	177	112	63	98	116	130	106	131	110	11·6	11·6	18	93
(F) V. narrow short (gracile)	172	108	62	96	**110**	126	**104**	**125**	107	12·0	12·4	18	89
(G) V. narrow v. robust	180	114	64	99	116	130	109	129	**106**	12·5	12·5	24	85
(H) (Narrow) (long) (robust)	186	118	67	103	121	136	113	134	115	12·1	12·4	22	94
(I) V. narrow v. long v. robust	190	119	**69**	104	119	133	113	128	108	**13·3**	**14·0**	**25**	**79**
(J) V. long robust	—	—	—	—	—	—	—	—	—	—	—	—	—
(K) Broad (long) (robust)	189	121	68	104	127	**140**	115	142	121	12·0	12·2	19	100
(L) V. broad v. long robust	**195**	**124**	68	**108**	**132**	140	**118**	**146**	**127**	11·6	11·8	20	99

In bold, maximum and minimum mean values observed.

5) is very similar, 65·2% Australians, 21·7% Afalou/Taforalt, 8·7% Fueguian/Patagonian and 4·3% Ainu. Among the crania along the axis of the relationship, which are neither particularly robust or gracile, those towards the upper right quadrant are mainly Australian, Fueguian/Patagonian or Afalou/Taforalt. These populations can be said to be comparatively robust among recent modern humans (Figure 9). The group of skulls circled in the lower left quadrant of Figure 3, i.e. small and gracile crania, are 44 in all: 13 Africans (29·5%), 13 Eastern Asians (29·5%), 11 Southeast Asians (25·0%) and seven Europeans (15·9%). The crania identified as gracile in terms of facial features (circled in the lower left quadrant of Figure 5) are 34 in total: 11 African (32·3%), nine Southeast Asian (26·5%), six East Asian (17·6%), three Europeans (8·8%), two Inuit (5·9%), one Indian (2·9%), one Australian (from the northwest—2·9%) and the fossil of Nahal Ein Gev, from Israel. These populations, the majority of recent populations, may be considered relatively gracile within present day cranial variation.

The regional origin of the crania identified as either too robust or too gracile for their size in Figure 3, i.e. crania that do not follow closely the relationships size/robusticity identified in the canonical correlation, does not help to understand why they depart from the main pattern. Among those skulls that show greater robusticity than expected for their size, we find two Southeast Asians, one African, one Amerindian, four Europeans, one Natufian, one Fueguian/Patagonian, and three Australian. Among those that may be said to be relatively large for their gracility we find three Afalou/Taforalt, three Fueguian/Patagonian, Zkn UC 103, four Africans, and one Polynesian skull. The fact that some of the individuals that are too robust or too gracile for their size in Figure 3 fall within the robust or gracile groups of facial features in Figure 5, would suggest that certain individuals show different patterns of gracility/robusticity for different functional complexes, and thus depart from an overall cranial pattern.

Sexual dimorphism

Sexual dimorphism is an important factor in the expression of robusticity, and it may affect the interpretations presented here in two ways. First, it is possible that the relationship between cranial dimensions and robusticity varies between males and females. The crania used in this study are unsexed, and therefore, this possibility cannot be assessed. Nevertheless, the relatively small dispersion of data points, for each regional group, along the canonical correlations would suggest that the male and female crania contained in the sample behave in a similar way. On the other hand, it is possible that biased regional samples towards males or females are affecting the identification of populations as robust or gracile, while if the regional samples were sexually balanced maybe each population would cover the range of variation in robusticity. In order to investigate this possibility, two sexed series, one a relatively gracile group, Inuits, and the other a robust population, Fueguians, were examined. The skulls were sexed using features of the mandible, orbital sharpness and whenever possible, post-cranial information. Each skull was given a ‘‘robusticity score’’ representing the sum of the grade scores of development of the supraorbital ridges, zygomatic trigone, infraglabellar notch, zygomaxillary tuberosity, sagittal keeling, frontal keeling, occipital torus, occipital crest and external occipital protuberance, and the variation in the two populations compared (Figure 10). From these data it is clear that females are more gracile than the males of their own population, although there is overlap between the sexes (more in Inuits). However, the gracile and robust character of each group is maintained. Male Inuit skulls show ‘‘robusticity scores’’ similar to female Fueguian crania and no Inuit skull is as robust as Fueguian males. Plotting

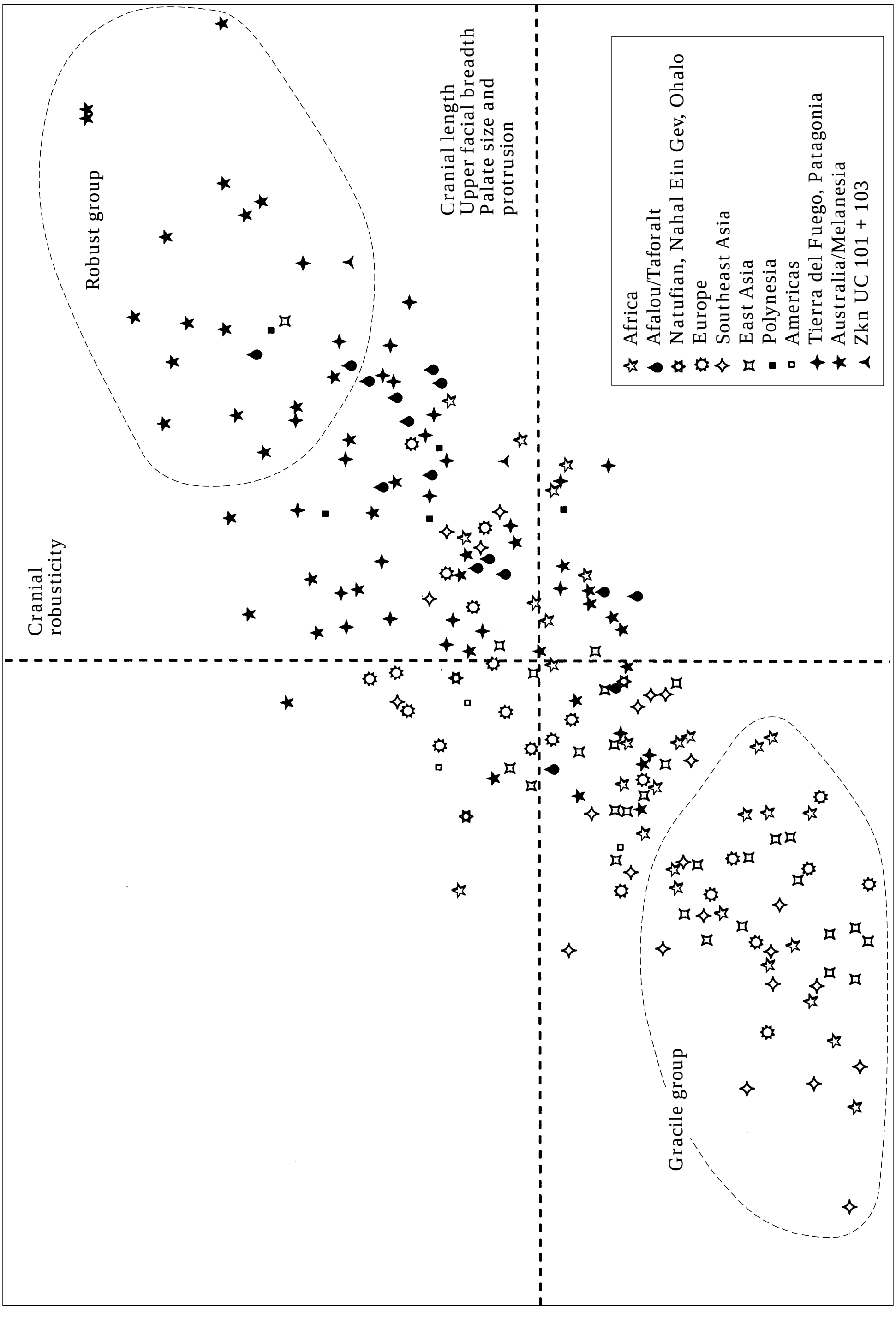


Figure 9. Identification of the crania on Figure 3 by region of origin, showing that cranial robusticity among recent humans is largely found in Australian, Fueguian-Patagonian and Afalou-Taforalt crania.

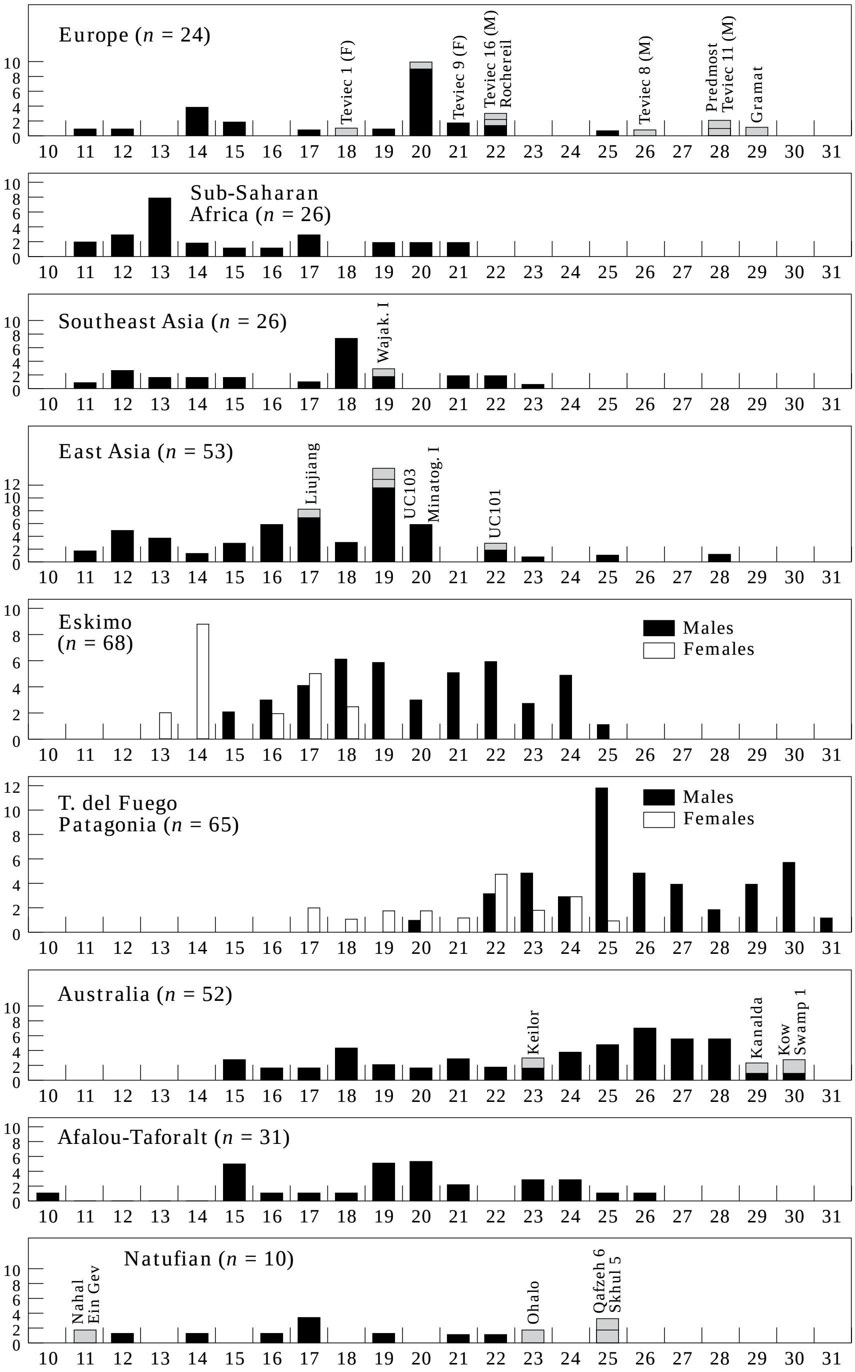


Figure 10. Differences in robusticity between male and female Eskimo and Fueguian skulls, and comparison to the distribution of levels of robusticity within modern populations (Europe, sub-Saharan Africa, Southeast Asia, East Asia, Australia, Afalou-Taforalt, Natufian) and certain Upper Pleistocene modern fossil specimens. Robusticity expressed as an individual score representing the sum of the ordinal grades of development of the supraorbital ridges, zygomatic trigone, infraglabellar notch, zygomaxillary tuberosity, sagittal keeling, frontal keeling, occipital torus, occipital crest and external occipital protuberance.

the ‘‘robusticity scores’’ of the unsexed populations used in this study (the complete series) further confirms the identification of gracile (sub-Saharan African, Southeast Asian, East Asian, European, Natufian) and robust (Australian, and to a less extent Afalou/Taforalt) groups, with fossil European crania falling in the robust end of the scale (Figure 10).

Figure 11 shows the identification by population of the crania along the orthogonal plot of the first and second principal components (Figure 7). Horizontally, along the axis of PC1 (correlated with size—maximum cranial length: GOL; bijugal, bifrontal, biorbital, maxillary, orbital and zygomaxillary breadths: JUB, FMB, EKB, MAB, OBB, ZMB; basion–nasion length: BNL) we observe small and gracile (left) to large and robust (right) morphologies, while vertically along the axis of PC2 (positively correlated with parietal and frontal breadth: XPB, XFB; negatively correlated with position of minimum frontal breadth: WFBZFS, palatal length: PALL, dental size: BLM1 and BLM2, and robusticity: ST, IN, TR, RO, SK) the broad crania (upper half) are separated from the relatively narrow skulls with large teeth (lower half). Three interesting points are disclosed by the geographical distribution seen in Figure 11. First, the group of crania in the upper left quadrant that may be described as broad, short and gracile, is mainly composed of Asians (Southeast and East Asians 52·8%), Europeans (16·7%), and to a lesser degree, Africans (13·9%). Second, the three skulls furthest to the left along PC1 are an Andaman Islander, a bushman and an individual from Sarawak. They show a very extreme morphology in relation to all other crania, and through their diverse origins, show that extreme gracility in terms of both size and shape, has been achieved in several modern human groups. And third, it is possible to identify the broad–robust (right upper quadrant) from the narrow–robust crania (right lower quadrant). The combination of large size, breadth and robusticity may be found in individuals from all populations except the Australians, although the majority is formed by the Afalou/Taforalt (22·7%), many of the Fueguian/Patagonian (20·4%), and many African (13·6%), European (13·6%) and East Asian skulls (13·6%). A few skulls from diverse regional origins (two Southeast Asians, two African, one Fueguian, one Polynesian and the Zkn UC 103 fossil), are long and robust but comparatively narrow, although the differences with the group of long, broad and robust crania are not very pronounced. However, all the Australian crania are considerably narrower than the rest of skulls analysed, forming a clear cluster at the bottom of Figure 11. Australian crania depart from the main pattern in that pronounced robusticity is observed not only in very large skulls. The group of crania identified as G in Figure 7 is not particularly large, and yet presents high levels of robusticity. Their distinctive feature is the small width of the vault.

In summary, the results of the previous analyses show that:

(1) There is a close relationship between overall cranial robusticity (including facial and occipital traits) and cranial size whereby variation in the metrical dimensions has an effect on the expression of robusticity.

(2) There is an even closer relationship between facial robusticity and craniodental dimensions.

(3) The main metrical factor underlying these relationships is size, in particular cranial length, upper facial breadth, facial–basal length, palatal size and dental dimensions.

(4) A secondary metrical factor is related to cranial shape, contrasting broad gracile skulls with narrow robust ones.

(5) The integration of the two components of variation, size and shape, disclose 12 anatomical combinations with differing levels of robusticity.

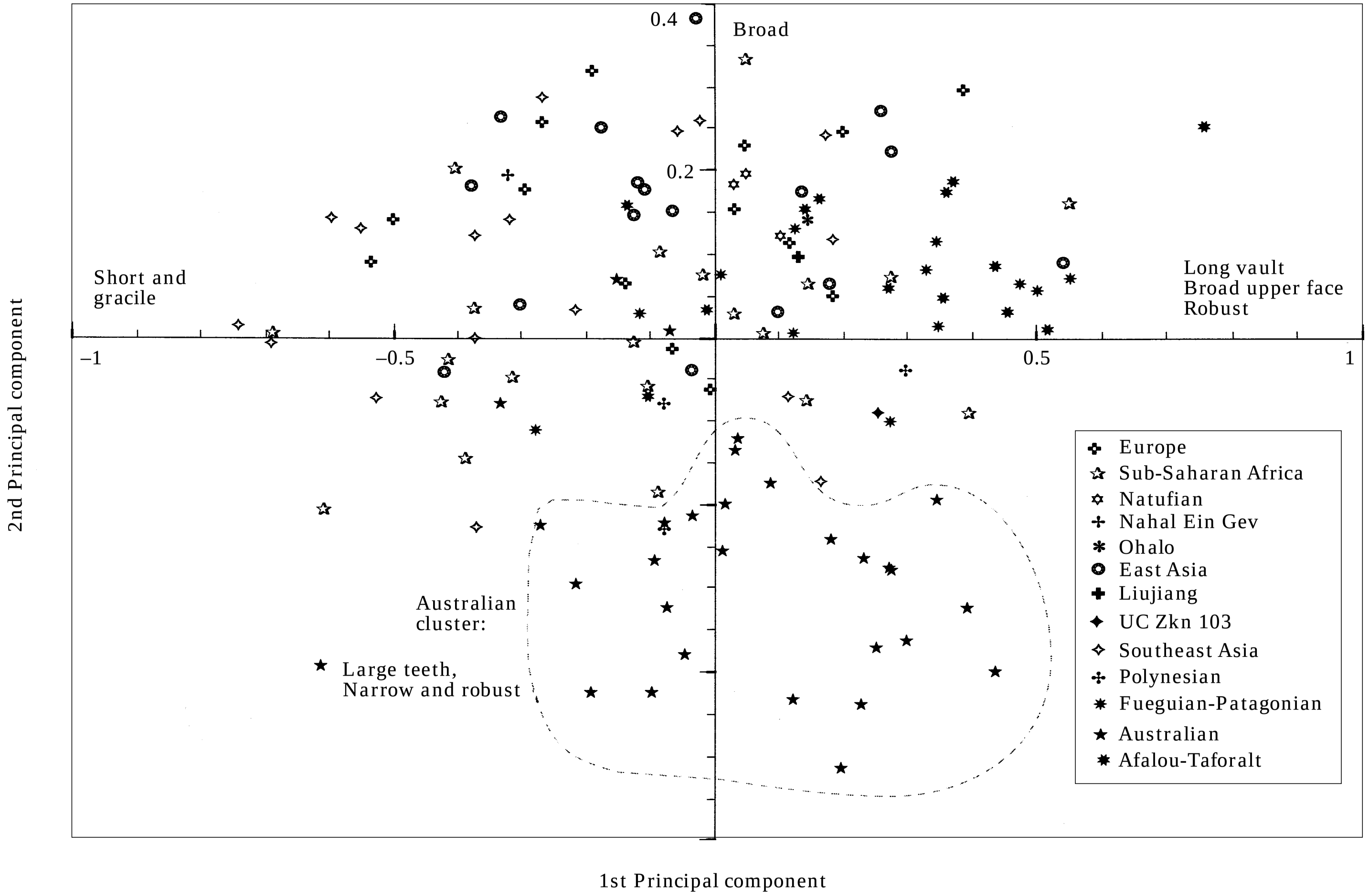


Figure 11. Identification of the crania on Figure 7 by region of origin, showing the relationship between robusticity and pronounced narrowness of the skull is almost uniquely found in Australia.

(6) There is a clear geographical pattern to craniofacial robusticity among recent humans, whereby the robust skulls from Australia, Tierra del Fuego, Patagonia, Afalou and Taforalt are contrasted with the gracile character of most recent populations.
(7) Most robust individuals present absolute large size, in both length and breadth of the vault, except for Australian crania that are robust and narrow.

Discussion

Functionality

The results obtained in this study indicate that spatial relationships of craniofacial form are the most important correlates to robusticity. The amount of variance in robusticity (taken as a single complex) explained by metrical dimensions varied from 25–40%. Two anatomical relationships of robusticity are identified, one in terms of cranial size and another one in terms of cranial shape. The relationship with the group of variables that represent size is the stronger of the two. The anatomical parameters of the complex representing cranial size remained stable in all the analyses performed, and may be characterized as comprising cranial length, upper facial breadth, facial–basal length, palatodental dimensions and basal breadth. The level of cranial and facial robusticity (expressed in terms of the size of the supraorbital ridges, zygomatic trigone, zygomaxillary tuberosity, occipital torus, depth of the infra-glabellar notch and sagittal keeling) increases as the variables within the size complex increase in value. This relationship identifies a group of skulls that are either very robust or very gracile (upper and lower quadrants of Figures 3 and 5), the robust crania being on average 8–12% larger than the gracile ones. These two groups of skulls, very robust and very gracile, do not differ in relation to mean cranial and frontal breadth, although all gracile crania are relatively broad (XPB: CV = 4·4), whereas robust skulls may be broad or narrow (XPB: CV = 7·3). The relationship of cranial robusticity with a *shape* complex, identified through the PCA, contrasts gracile crania with broad frontals and parietals with robust narrow skulls that also have very large teeth, palates and a relative backward position of minimum frontal breadth. This relationship is independent of size as described above.

The combination of the size and shape factors that constrain the expression of cranial robusticity define a number of anatomical groups of skulls that follow specific parameters in terms of cranial breadth, size and robusticity. Two different anatomical circumstances in which cranial architecture needs superstructures can be recognized (a) in very long skulls with broad upper faces and large palates (independent of the breadth of the vault), and (b) in very narrow skulls with large teeth (independent of cranial length and upper facial breadth). The group that presents the greatest robusticity is one that combines these two conditions, i.e. very long and narrow skulls, with broad upper faces and large teeth. It is possible to classify crania into robust and gracile groups, which may be divided into six categories:

Gracile crania		Robust crania
very small	(a)	very large
small and very narrow		very large and very broad
small and narrow		large and broad
small and ± broad		large and ± narrow
small and broad		very large and very narrow
very broad	(b)	very narrow

Studies on the relationship of each feature of robusticity and craniodental dimensions through discriminant analyses found that the expression of each trait may be predicted with ca. 100% accuracy (Lahr, 1992, 1996). The difference with the results obtained here, which reveal a relationship common to all cranial superstructures, suggest that the functional size/shape constraints are strong, but vary in their determination for each trait. Although this study did not explore the biomechanical relations between metrical dimensions and the superstructures, it shows through the redundancy values that it is the dimensions of a skull that affect the expression of robusticity, while the latter has little effect on the metrical parameters. The close relationship between palatodental size and facial robusticity is clearly seen in the plot of variables along the first and second principal components of variation (Figure 6). This association gives support to the functional interpretation of the facial superstructures in terms of resistance to masticatory stress and the potential effects of localized stress on the development of a particular superstructure (Endo, 1970; Russell, 1983, 1985; Demes & Creel, 1988; Hilloowala & Trent, 1988*a*,*b*). Russell (1985) argued that the moment arm of the downward pulling force of the temporalis is represented by the distance from mid-face to the temporal fossae. Russell (1985) used minimum frontal breadth to represent this dimension. It is possible that bifrontal breadth, biorbital breadth and bijugal breadth represent equivalent dimensions, by which the breadth of the upper face relates to the necessary strength to produce effective muscle forces, and affects robusticity as part of the *size* complex identified in this study.

Therefore, the results from the present study could be interpreted as suggesting that each of the features of robusticity that form the cranial superstructures has a specific relationship with the muscular and masticatory forces acting on the skull, but that they also form a single functional complex, with common underlying anatomical constraints that explain about 40% of the variation observed.

Regionality

Among modern populations, there is a marked regional pattern of expression of cranial robusticity and its anatomical correlates—cranial length and breadth, upper facial breadth and palatodental size. Although Figures 3 and 5 show that recent modern variation in robusticity forms a gradient from extremely gracile to extremely robust, the distribution of populations along this gradient (Figure 9) is not gradual. This becomes clear when the percentage of crania from each region in each of the four quadrants of Figures 3 and 5 is calculated (Table 4). The results confirm visual observations of robusticity, and separate recent populations on the basis of integrated metrical and non-metrical parameters: the large and robust groups—Australo-Melanesians and Fueguians-Patagonians—from the small and gracile ones—sub-Saharan Africans, Southeast Asians and East Asians. The Europeans fall in between the extremes, with a relatively large number of cases of robust facial features, although not presenting any case of pronounced robusticity (i.e. circled in the upper right quadrant of Figures 3 and 5). The sample sizes of Polynesians, Inuits and Ainu are too small to allow characterizations of these groups. However, the findings again confirm visual observations, with the New Zealand and Ainu crania falling within the parameters of the robust populations (upper right quadrant), and Inuit within the gracile ones (lower left quadrant). Of the Pleistocene and early Holocene modern fossils included, the majority of the Afalou/Taforalt are clearly robust, as are the Zhoukoudian UC 101 and 103 remains, whereas the Middle Eastern late Upper Palaeolithic (Ohalo, Nahal Ein Gev), and especially the few complete Natufians, tend to be more gracile. A further distinction can be made. As mentioned above, cranial robusticity is expressed in very

Table 4 Regional distribution of crania in Figures 3(a) and 5(b)

(a) Percentage of crania in each of the four quadrants of Figure 3 by region

Aus/Mel: 40		Fue/Pat: 26		Af/Taf: 16		African: 29		SE.As.: 22		E. Asian: 26		Europe: 21	
2 5·0%	27 67·5%	—	21 80·8%	—	12 75·0%	1 3·4%	3 10·3%	1 4·5%	3 13·6%	3 11·5%	2 7·7%	7 33·3%	3 14·3%
5 12·5%	6 15·0%	2 7·7%	3 11·5%	2 12·5%	2 12·5%	20 69·0%	5 17·2%	18 81·8%	—	20 76·9%	1 3·8%	11 52·4%	—

(b) Percentage of crania in each of the four quadrants of Figure 5 by region

Aus/Mel: 29		Fue/Pat: 13		Af/Taf: 13		African: 22		SE.As.: 18		E. Asian: 12		Europe: 12	
—	23 79·3%	—	10 76·9%	1 7·7%	10 76·9%	1 4·5%	3 13·6%	1 5·5%	3 16·7%	—	1 8·3%	2 16·7%	5 41·7%
4 13·8%	2 6·9%	1 7·7%	2 15·4%	2 15·4%	—	17 77·3%	1 4·5%	13 72·2%	1 5·5%	10 83·3%	1 3·8%	5 41·7%	—

Aus/Mel, Australo-Melanesian; Fue/Pat, Fueguians-Patagonians; AF/Taf, Afalou/Taforalt; SE.As., Southeast Asian; E. Asian, East Asian.

large skulls (a) and in very narrow ones (b). In terms of regionality, the striking feature is that the separation of modern crania along the large–robust/small–gracile dimensions is applicable to all populations but the Australo-Melanesians. The latter population follows certain parameters of its own, by which robusticity becomes relatively decoupled from cranial size to follow a closer association with cranial breadth and dental size. In this respect, Australo-Melanesian crania are different from most modern human skulls.

Although sexual dimorphism in most modern groups is expressed as different levels of robusticity in males and females, the different ranges of variation in robusticity observed in two series of sexed skulls shows that within-population variation due to sexual dimorphism is less important than the general metrical and non-metrical parameters of the population as a whole.

Phylogenetic interpretations

Although ontogenetic bone remodelling due to localized biomechanical stress probably affects the full development of cranial superstructures, the distinct regional patterns in robusticity cannot be explained solely by differential dental loading or para-masticatory use of the dentition in currently robust populations. In his comment on Russell's work, Turner II (1985) argued this point clearly by stating that the populations that load their teeth the most—the Eskimos—are not amongst the more robust. Furthermore, recent studies on *in vivo* bone strain analysis have shown that masticatory forces do not create sufficient strains on the supraorbital area of primates to account for supraorbital torus development (Hylander *et al.*, 1991). Multivariate analyses of modern human variation have shown that main cranial dimensions reflect the genetic differentiation of modern groups throughout the Upper Pleistocene. Therefore, it may be assumed that variation in these dimensions, which would affect the expression of cranial robusticity, are largely of a genetic basis. It is suggested that cranial size and robusticity, and to a lesser degree cranial shape and robusticity, form functional complexes that co-varied along the evolution of present cranial diversity through varying dimensional changes in the different populations.

Accepting that size/robusticity form an evolutionary unit of covariance, the present regional pattern of robusticity could still be the result of either phylogenetic or purely functional processes. Functionally, it is possible that as dental size and the size of the muscles of mastication (especially the size of the temporalis which is closely associated to cranial length) reduced during the late Pleistocene, an entire functional complex was released, and robusticity was lost in all populations that underwent this process. If this was the case, then the distribution of robusticity and its anatomical correlate of size does not carry any phylogenetic information, because it could have occurred in parallel in most modern populations. However, the association of loss of robusticity with technological developments is not straightforward. Among hunter–gatherer groups like !Kung bushmen, Inuit, Australians, Onas or Tehuelches, the whole range of levels of robusticity are observed. Brace (1979) suggested that cooking was the main technological development that released the pressure on the masticatory apparatus, but the use of fire and some pre-masticatory preparation of food apply to all recent populations, gracile or robust. Furthermore, dental reduction in southeastern Australia during the early Holocene occurs without any indication of technological developments (Brown, 1992). Therefore, the incongruence between the mechanical sources of stress in a population and its expression of robusticity would suggest that mechanisms other than the release of a selective pressure acted upon the gracilization of the modern skull.

If craniodental dimensions are in fact more genetically constrained, its reduction in later Pleistocene populations would have resulted from specific adaptations, which although homologous in most regions because of similar physical constraints of the skull and technological developments, would be indicative of phylogenetic relationships among modern groups through their spatial and temporal pattern. This is consistent with the results of multivariate analyses, which show that although most recent populations have undergone a size reduction in relation to earlier modern fossils (Kidder *et al.*, 1992; Lahr, 1996), a unique combination of cranial dimensions allows the identification of most human groups (Howells, 1973, 1989; Brace *et al.*, 1990; Pietrusewsky, 1990, 1992; Wright, 1992).

If an epigenetic basis for cranial superstructures is accepted, cranial gracilization in most recent populations and on the other hand, the retention of robusticity in a few groups, could be examined through the fossil record of modern humans.

Although the definition of modern cranial form is a controversial subject (Day & Stringer, 1982; Wolpoff, 1986; Brown, 1990; Lahr, 1996), it is generally agreed that a modern skull should present a relatively small face tucked under the vault that is relatively short and high, a relatively vertical forehead, parietal enlargement, a relatively rounded occiput, a flexed cranial base, a canine fossa, an occipital protuberance in the occipital bone and mental eminence or chin. Most descriptions of modern *H. sapiens* would also include skeletal gracility as characterizing the group. The characterizations described above relate mainly to cranial shape rather than size, and are observed in a group of skulls from the early Upper Pleistocene of Africa and Israel at the exclusion of other hominid populations of possible similar age, like the Neanderthals or the Ngandong sample (Stringer, 1993). However, these early modern fossils are considerably larger and more robust than most recent humans. Kidder *et al.* (1992) estimate that the early modern sample of Skhul and Qafzeh and the early Upper Palaeolithic hominids of Europe are from 10–30% larger in main cranial dimensions than recent Europeans. The larger size and more pronounced robusticity in the early modern sample are consistent with the results obtained in this study, by which the metrical dimensions of all early modern fossils imply higher levels of cranial robusticity than most recent populations. The ancestral condition for early modern humans is one of large size (in both breadth and length) and robusticity, and the later differentiation of populations must have occurred partly through reduction along these parameters. It follows that a modern cranial ‘‘shape’’ appeared before cranial size reduction and gracilization occurred, and a definition of a modern human skull cannot include cranial gracility among its parameters.

There is still the case of the distinctiveness of the Australian sample. Table 5 presents the value of the metrical variables with moderate to high loadings on the first and second principal components in a group of late Middle Pleistocene and early modern fossils. When comparing the values in Table 5 with those of Table 3 (the dimensions of the 12 anatomical groupings defined by the plot of the first and second PCs), it is evident that early modern fossils are large and robust, but also broad. Although they are not complete enough to be included in the multivariate analyses, they present values which are most consistent with the groups in the upper right quadrant of Figures 7, 8 and 11 (groups L or K). Therefore, the distinctive anatomical combination present in Australian crania of a very narrow vault and pronounced robusticity, does not represent a plesiomorphic state. They do not share these anatomical parameters with either the early modern sample from Africa/Israel nor with the Ngandong sample from Java. Current dates for the occupation of Australia suggest a very early entry into the continent (Roberts *et al.*, 1990), and both archaeological and morphological data are compatible with a subsequent period of relative isolation (Kirk, 1981). A possible explanation

Table 5 Individual values of late Middle and Upper Pleistocene fossil specimens for the metrical variables correlated with cranial robusticity

	Neand.	Afr. 'a' H.s.		Early moderns						Afr. Ple./Hol/moderns				M. East Ple/Hol moderns			
	La Ferras.	Dj. Irh.	LH 18	Omo I	Flor.	Skh.V	Skh.V	Qaf.6	Qaf.9	Afa/Taf.	F.Hoek	Elm. A	Elm. B	NEGev	Ohalo	Ein Gev	Natuf
GOL	207	198	203	209	(202)	191	205	194	195	190·2	198	190	197	177	182	186	190·3
JUB	126	—	—	—	(135)	130	—	131	129	123·6	120	123	124	(121)	122	—	116·5
FMB	113	(100)	—	117	124?	114	—	115	108	105·8	102	100	101	100	107	99	100·2
EKB	112	—	—	114	117	114	—	—	108	103·5	100	102	101	100	104	—	97·9
NOL	204	176	200	200	—	182	—	185	—	185·3	192	186	195	176	181	184	188·1
MAB	86	—	71	—	—	70	73	71	70	69·2	61	68	65	61	67	—	63·3
BNL	123	—	—	—	—	96	—	—	—	105·4	94	101	101	89	98	88	100·0
OBB	46	47	—	—	51	49	—	46	43		40	40	40	39	43	—	
ZMB	112	114	—	—	105?	102	116	106	107	101·3	101	103	101	89	94	—	96·8
AUB	145	143	123	131	—	130	130	130	124	128·3	123	122	128	121	125	124	122·8
BBH	129	—	—	—	—	121	—	—	—	140·3	128	130	140	129	133	125	138·2
FRC	119	108/127?	116	130	110	108	120	120	117	114·1	122	116	126	114	110	124	113·9
XPB	159	151	136	—	(151)	142	146	144	141	143·4	146	129	146	(137)	143	148	137·7
XFB	125	(122)	115	—	137	115	—	127	118	122·3	119	111	127	(124)	129	—	118·7
SILLPA	—	109	89	—	125?	91	106	112	114	97·1	—	—	—	109	120	—	106·7
BLM1	—	—	—	—	—	—	12·9	12·3	13·3	12·2	—	—	—	11·8	12·5	—	12·4
BLM2	—	—	—	—	—	—	12·3	12·5	12·5	12·7	—	—	—	12·0	12·6	—	12·5
SSS	38	32	—	—	22?	27	27	23	28	22·4	22	26	26	22	22	—	23·7
PALL	—	—	57	—	60?	67	60	65	61	56·1	—	—	—	52	57	—	56·4
WFBZF	—	25/22	− /24	23/26	22/24	22/24	23/27	22/25	15/17	23/21	—	—	—	9/12	13/14	17/17	15·6
GLS	7	79	7	8	5	11	—	12	—		4	6	3	6	11	7	2·4

	Eu. Ple./Hol. moderns											SEA + EA Ple./Hol/moderns					
	Cro-M.	Mlad.	PreD.III	Pred.IV	Grim.	Chanc.	Ab Pat.	M. Gora	Muge	Tev. 11	Tev. 16	Wadjak	UC 101	UC 103	Liuj.	Min I	Min. IV
GOL	205	200	203	193	194	196	182	178	178·9	190	186	205	205	187	191	178	203
JUB	133	116	125	117	120	123	114	116	110·0	125	127	131	126	128	120	128	124
FMB	111	102	110	98	94	104	99	104	93·9	102	101	113	109	108	101	103	110
EKB	112	102	109	101	100	101	97	104	93·5	102	102	113	109	107	101	106	109
NOL	199	194	198	188	189	195	179	174	176·5	184	182	199	199	182	188	175	198
MAB	69	68	68	60	66	60	64	63	63·0	72	66	70	69	67	66	67	68
BNL	104	104	109	100	95	116	97	98	97·3	109	105	95	108	108	105	90	109
OBB	48	41	46	42	39	43	38	42	41·9	44	44	41	45	44	39	43	46
ZMB	106	102	98	89	92	96	98	94	93·3	107	106	115	105	100	99	101	98
AUB	125	127	139	131	126	127	122	118	113·8	125	126	140	136	124	124	125	139

Continued overleaf

Table 5 *Continued*

	Eu. Ple./Hol. moderns											SEA+EA Ple./Hol/moderns					
	Cro-M.	Mlad.	PreD.III	Pred.IV	Grim.	Chanc.	Ab Pat.	M. Gora	Muge	Tev. 11	Tev. 16	Wadjak	UC 101	UC 103	Liuj.	Min I	Min. IV
BBH	135	138	133	134	137	151	129	128	131·1	150	140	136	135	145	136	132	133
FRC	123	115	120	115	117	114	110	101	105·6	117	111	113	114	107	118	101	120
XPB	152	142	147	145	135	139	138	127	128·6	139	143	150	143	127	144	147	147
XFB	130	129	131	122	114	125	118	111	108·3	122	121	122	121	123	123	112	131
SILLPA	—	—	112?	—	—	—	—	—	—	—	—	103	76	84	92	93	112?
BLM1	—	—	13·2	—	—	—	—	—	—	—	—	13·9	—	12·7	·13·0	—	13·2
BLM2	—	—	12·7	—	—	—	—	—	—	—	—	13·9	12·3	11·9	·13·2	11·9	12·7
SSS	22	23	30	24	28	25	26	25	25·2	29	29	25	23	25	20	21	30
PALL	—	—	62	—	—	—	—	—	—	—	—	63	55	58	50	51	62
WFBZF	—	—	19/18	—	—	—	—	—	—	—	—	27/20	22/20	16/16	18/20	25/23	19/18
GLS	5	5	7	5	3	3	4	5	3·1	6	4	7	7	5	4	7	7

	Australian Ple./Hol. moderns						Ngandong						
	Mungo I	Mung.III	K. Sw. 5	Keilor	Kanalda	Coob. C.	Solo I	Solo IV	Solo V	Solo VI	Solo IX	Solo X	Solo XI
GOL	—	191	191	199	189	190·8	190	—	214/219	192	192	193/202	197/200
JUB	—	—	122	126	126	—	—	—	—	—	—	—	—
FMB	[107]	—	103	108	108	[113·3]	—	(102)	—	—	—	—	—
EKB	97	—	100	107	103	106·2	—	—	—	—	—	—	—
NOL	—	—	187	197	185	—	186	—	211/216	191	—	—	198
MAB	—	—	72	72	80	70·8	—	—	—	—	—	—	—
BNL	—	—	—	110	107	102·4	—	—	—	110	—	—	114
OBB	—	—	41	43	45	43·7	—	—	51	—	—	—	—
ZMB	—	—	101	103	102	100·2	—	—	—	—	—	—	—
AUB	—	—	115	134?	129	124·9	—	—	144	129	147	148	138
BBH	—	—	—	(142)	144	139·2	—	—	—	123	—	—	124
FRC	—	—	117	112	118	117·6	116	112	125	115	114	118	112
XPB	130	132	137	144	142	135·5	146	140	147	139	146	147	138
XFB	—	—	114	129	118	—	119	118	127	117	(116)	123	120
SILLPA	—	—	(107)	105	101	—	(110)	94	102	108	98	91	102
BLM1	—	—	—	13·3	13·6	—	—	—	—	—	—	—	—
BLM2	—	—	—	—	14·2	—	—	—	—	—	—	—	—
SSS	—	—	25	26	27	—	—	—	—	—	—	—	—
PALL	—	—	61	67	62	62·5	—	—	—	—	—	—	—
WFBZF	—	—	22/22	30/29	33/33	—	− /(46)	23/36	30/38	25/32	28/39	26/40	29/37
GLS	—	—	5	3	5	—	(8)	—	9	5	—	—	5

for the Australian morphology is that during a comparatively long period of isolation and varying demographic parametres (Smith & Sharp, 1993), this population underwent significant morphological differentiation as it adapted to late Pleistocene Australia. In terms of evolutionary pathways, diversification subsequent to the original adaptations would be responsible for the complex mosaic pattern of constancy in some features and pronounced heterogeneity in others observed among more recent aboriginal groups.

Implications for modern human origins

Because several of the features of robusticity examined in this study have been advocated as evidence for regional continuity in southeast Asia, the results obtained have important implications for the on-going debate about the origins of modern humans.

First, it was shown that the cranial superstructures respond to a functional complex, i.e. although they may vary in their total independent expression, their incidence is correlated and they respond to common underlying factors. This means that, on a worldwide basis, a skull with large supraorbital ridges is likely to have large zygomaxillary tuberosities, large zygomatic trigones, deep infraglabellar notches, and even occipital tori. These results strongly reject the use of each of these features independently as phylogenetic markers (Wolpoff *et al.*, 1984; Frayer *et al.*, 1993). Furthermore, these results also invalidate suggestions that the combined occurrence of all these markers in Australian skulls carries phylogenetic weight (Habgood,1989), for it is now shown that the expression of these features is correlated.

Second, the geographical pattern of cranial robusticity among recent humans shows that although most populations have undergone a process of reduction in cranial size accompanied by loss of cranial superstructures, this process has not been universal. Furthermore, Pleistocene modern fossils are comparatively larger and more robust than most recent humans, a pattern that is consistent with the relationship between cranial size and robusticity identified in this study. Therefore, both the spatial and temporal patterns of size and robusticity highlight the need to disassociate the definition of a modern cranial form from levels of robusticity. Arguments that early Upper Pleistocene African fossils are not ‘‘modern’’ based on high levels of robusticity do not apply.

And last, these analyses show that Australian cranial morphology, at the centre of the debate about modern human origins, is indeed an outlier among modern anatomical patterns. However, the results also suggest that the Australian pattern does not result from the retention of a plesiomorphic combination of cranial dimensions and robusticity that would associate them to the Ngandong hominids. Although the cranial superstructures are in themselves plesiomorphous for all modern humans, the anatomical parameters that constrain their expression in Australian crania are a characteristic of this group. The most likely explanation for their distinctiveness probably lies in the early occupation of Australia and subsequent differentiation within the continent. Wright (1976) suggested a similar evolutionary mechanism of local response to selection once in Australia to explain large dental size in the late Pleistocene Aboriginal population of this continent.

Conclusions

The present study was carried out to examine the existence of a relationship between cranial metrical dimensions and levels of robusticity. The results obtained show that many of the superstructures of the skull have a correlated expression, so that cranial robusticity may be treated as a morphological complex by which the probability of a skull presenting not one but several superstructures is high. The canonical correlation analyses showed that there is a relationship between this morphological complex ''*robusticity*'' and cranial metrical dimensions, which remained constant as the major component in all analyses. Furthermore, the analyses show that although the dimensions of the skull affect the development of cranial superstructures, the latter have a much less important effect on the metrical parameters. The main correlate to robusticity is cranial *size*, in particular cranial length, upper facial breadth, facial–basal length and palatodental dimensions. The results from the canonical correlations allow the identification of robust and gracile groups of crania, the former between 8–12% larger than the latter. PCA revealed that there is also a less important relationship between cranial robusticity and *shape* of the skull, contrasting broad gracile skulls with narrow robust ones with large teeth. An orthogonal plot of the cranial sample along the first two principal components shows that the combination of the *size* and *shape* parameters separates the broad from the narrow robust skulls.

A canonical correlation analysis using only the features of facial robusticity obtained a stronger relationship with size than when including all the superstructures studied. These results, together with previous findings of stronger relationships between each cranial superstructure and metrical parameters, suggest that although there is a ''*robusticity*'' complex with common underlying parameters, each of the features within this complex responds to specific cranial dimensions and mechanical forces for their full expression. Although both phylogenetic and ontogenetic processes act through developmental mechanisms based on functional relationships, the correlation of robusticity with dimensions that characterize different human populations suggests that there are strong phylogenetic processes involved in determining the expression of cranial superstructures.

Consistent with the results obtained from recent modern humans, early modern fossils show a combination of great robusticity and large size along the parameters identified in these analyses, both in terms of cranial length/upper facial breadth and cranial breadth. This combination is still present in relatively late Pleistocene fossils, like the Zhoukoudian Upper Cave and the Afalou/Taforalt samples. Among recent modern populations, most groups have undergone a process of gracilization in size and superstructures, with a few exceptions like Fueguian, Patagonian, some Ainu and to a lesser degree some European crania, which still show great size and relative robusticity. Australian crania are also robust, but differently from the above mentioned groups, robusticity in this group is associated with very narrow skulls, some of which are not particularly large. This distinctive pattern in Australia is not related to the retention of an ancestral condition because it is not found in conjectural ancestral forms, whether the early modern African/Middle Eastern samples or the Ngandong remains.

The correlation between robusticity and cranial dimensions highlights the need to study the cranial superstructures within the context of metrical variation, and not individually as evidence of phylogenetic relationships.

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